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REPRODUCTIVE BIOLOGY OF PENAEID PRAWNS

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INTRODUCTION

In the contemporary period, knowledge of different aspects of reproduction in penaeid prawns is increasingly applied to improve their capture and culture fisheries. Information on process of maturation, distribution pattern and abundance of spawners, variations in fecundity and the relationship between the environmental factors and spawning has provided greater insight into the dynamics of population structure of these prawns in nature. Similarly, the rapid unfolding of facts governing the maturation process, biotic and abiotic requirements for successful breeding in captivity, and the advances made in the sexual and reproductive physiology and endocrinology have made it possible to achieve significant success in controlled breeding and brood stock development of these prawns for culture purpose.

FORMS OF REPRODUCTION

In penaeid prawns, the usual method of reproduction is by gametic reproduction participated by the gametes produced by the male and female parents. However, in certain species such as Penaeus kerathurus and Solenocera membranacea protandric hermaphroditism (Heegaard, 1967, 1971) or non-functional hermaphroditic specimens have occasionally been recorded.

SEXUAL DIMORPHISM

Perceptible sexual dimorphism in size and in certain external morphological features is exhibited by the penaeid prawns. Generally, the male penaeid prawn is smaller than the female. In the male, the endopods of first pair of pleopods are modified into a copulatory organ known as 'petasma' or 'andricum' and the second pleopod bears an accessory structure, the 'appendix masculina'. In the female, the sterinites of the last three thoracic somites are modified into protuberances, depressions or grooves, plates and sacs of diversified shape and features and referred to as 'thelycum'. The location of the external genital aperture also shows difference in the two sexes, it is being situated in the proximal podomere of the third leg in the female and on that of the fifth in the male. In certain species like P. setiferus the antennular flagellum and in P. californiensis third maxilleped also show sexual dimorphism.

The petasma and the thelycum besides serving as external genitalia, afford significant characters for the identification of different species of penaeids (Mohamed, 1970 a, b; George, 1970 a, b, c, d; Rao, 1970; Kunju, 1970). The petasma of penaeid prawns is symmatrical except in the species belonging to the genus Metapenaeopsis. In its general organisation it varies from simple to complex structure with the development and arrangement of the distal lobes.

Two types of thelyca are discernible in penaeid prawns: the open type with ridges and protuberances for the attachment of spermatophores and the closed type possessing two flaps (lateral plates) and enclosing a seminal receptacle where spermatophores are deposited.

GONADS

Testis

The primary reproductive organ of the male penaeid prawn consists of paired testes and vasa deferentia. The testes overlie the hind part of hepatopancreas and partly concealed by the heart. Each testis consists of an anterior lobe and 4 to 7 lateral lobes, and sometimes a short posterior lobe. The vasa deferentia arise from the posterior margin of the corresponding testis and runs beneath it to open to the exterior through the gonopore situated in the coxa of the fifth pair of legs.

Each vas diferens consists of four morphologically [redacted]istinct regions: the proximal, medial and distal regions, [redacted]nd a terminal ampoule. The proximal region is short and [redacted]rrow, and passes on to a thicker medial region which is [redacted]uble flexed or has the form of an inverted U-tube. The [redacted]ial region in P. kerathurus is further subdivided into [redacted]asal blind pouch, an ascending limb and a descending [redacted]. The descending limb of the medial region tapers to [redacted]latively long, narrow tube (distal vas deferens) which [redacted]nates in a dilated muscular region or terminal ampoule is [redacted], 1948; Malek and Bawab, 1974). The terminal ampoule is [redacted]shaped and divided into a conical apex, a large trunk [redacted]short cylindrical base. Subrahmanyam (1967) studying the male reproductive system of P. indicus distinguished a 'tubular portion' between the testis lobe and the vas deferens.

Ovary

The female reproductive organ consists of paired ovaries and oviducts. The ovary is situated dorsally and in the cephalothoracic cavity, it lies dorsal to the stomach and hepatopancreas. In a mature female, it extends from the base of the rostrum to the last abdominal segment. It is bilaterally symmetrical, each half consisting of a slender anterior lobe, a middle lobe in the form of 6 - 7 finger-like lateral lobules occupying the middle and posterior cephalothoracic region, and a posterior lobe extending the length of the abdomen. The two halves of the ovary are united at the base of the anterior lobe and at the tip of the posterior lobes in the sixth abdominal segment. The oviduct arises laterally from the tip of the penultimate lateral lobule of the middle lobe on either side and runs downward to the gonophore on the coxa of the third pereopod. The oviduct is short, thin and translucent (Rao, 1968).

GAMETOGENESIS

Male

Although information on various aspects of oogenesis, oosorption and oviposition (Adiyodi and Subramoniam, 1982) and on sperm morphology (Nath, 1941) and spermatogenesis in decapod crustaceans are available, detailed investigations on the phenomenon of oogenesis and spermatogenesis in penaeid prawns are limited. With the increasing application of artificial insemination and gamete preservation in the endeavour to evolve better strategies of culture of selected species and improvement of genetic stock, these aspects are receiving greater attention in the recent years.

On the basis of histological studies on the testis of *P. setiferus* King (1943) observed that the body of the testis is comprised of minute, convoluted seminiferous tubules which in the maturing shrimp contain spermatogonia and scattered nutritive or nurse cells. The spermatogonia have definite shape, large round nucleii surrounded by a mass of protoplasm, while the nutritive cells have irregularly shaped nucleii embedded in a syncitial mass of protoplasm with no cell boundaries. As the maturation process of the testis advances, the tubules increase in size and the spermatogonium passing through a period of quick growth becomes primary spermatocyte. The primary spermatocyte by a reduction division forms two secondary spermatocytes which through the formation of four spermatids develop into spermatozoa.

The sperm cells formed in the testes are released to vas deferens. As the sperm cells pass through the proximal region, they are converted into a compact mass with the participation of certain secretions by the glands of the vas deferens. This process is completed in the blind pouch. In the next stage, main layers constituting the spermatophoric [redacted] are formed around the sperm mass as it passes through [redacted] ascending and descending limbs of the vas deferens. When [redacted] spermatophoric mass reaches the terminal ampoule, protective [redacted] are added and eventually moulded into its final form. The detailed aspects of formation of sperm mass, spermatophores, [redacted] of the main layers of the 'body' and the 'wing' of [redacted] spermatophore and the role of secretions of vas deferens [redacted] by Malek and Bawab (1974) in *P. kerathurus.* In [redacted] Subrahmanyam (1967) observed that the tubular portion, the structure of which differs with the age of the prawn, has a generative portion and a lumen. The generative portion has follicles similar to those in the testis and presents spermatogonia, spermatocytes and sperms. However, this generative tissue is absent in males measuring above 170 mm.

SPERMATOPHORE

The spermatophore of penaeids such as *P. indicus*, *P. setiferus* mand *P. kerathurus* has a body which contains the sperm and a 'wing'. The wing serves for the attachment of the spermatophore in the thelycum. The spermatophores from each terminal ampoule are assembled into a pod-like structure soon after their expulsion. In *Parapenaeopsis stylifera* the spermatophore is oval and sac-like, measuring 0.06 mm in breadth and 0.3 mm in length. The sperms are arranged in 6-8 transverse compact rows.

SPERMATOZOA

The spermatozoan of the penaeid prawns is minute and composed of three parts: head, middle piece and tail. In *P. indicus* it measures 9.6 μ. The head is large, almost circular in outline, the middle region is short and slender, and the tail is relatively thick and short. In *P. stylifera*, however, the sperm differs in structure, being elongated and cylindrical with a very short tail. The head piece is smaller than the body and the tail. The whole spermatozoan appears to be enclosed in a thin transparent membrane which is produced into a spine-like process at the tail end (Shaikmahmud and Tembe, 1958).

Female

The ovary of *P. setiferus* (King, 1948) is composed of three layers, namely, an outer thin epithelium, a middle epithelium. The germinal epithelium which gives rise to oogonia is found to be confined to certain regions known as 'zone of proliferation'. The oogonia developing in the zone of proliferation pass through the primary and secondary oocyte stages and move in a column towards the centre of the ovarian lobe and then to the peripheral region. The mature oocytes get surrounded by the nurse or follicle cells. In the immature and early maturing stages the cytoplasm of the ova indicates basophilic reaction, and as the ova advance to mature stage, the cytoplasm becomes acidophilic. In immature ova no fat is present, but as they advance in development significant quantities of fatty yolk are formed.

The oviduct is made up of three layers. The columnar epithelium lining the lumen secretes lubricating fluid to facilitate passage of ova. The middle connective tissue layer is relatively thick while the outer epithelial layer is thin.

In the maturation process of the ovary, distinct changes in colour, size and texture take place making it possible to distinguish macroscopically different steps of maturation. Ovarian development has also been described in terms of histological appearance of ova (Oka and Shirhata, 1965) and Carotenoid content (Ceccaldi, 1968). Although the number of maturity stages described in literature varies from three to eight, most of the workers have distinguished five stages as follows:

<u>Immature stage:</u> The ovaries of immature prawns are thin, translucent, unpigmented and confined to the abdomen. They contain oocytes and small spherical ova with clear cytoplasm and conspicuous nuclei.

2. Early maturing stage: The ovary is increasing in size and the anterior and middle lobes are developing. The dorsal surface is light yellow to yellowish green. Opaque yolk granules are formed in the cytoplasm and partly obscure the nuclei. The developing ova are clearly larger than the immature stock.

3. Late maturing stage: The ovary is light green and is visible through exoskeleton. The anterior and middle lobes are fully developed. The maturing ova are opaque due to the accumulation of yolk.

4. Mature stage: The ovary is dark green and clearly visible through exoskeleton. The ova are larger than in the preceding stage and the peripheral region becomes transparent.

5. Spent-recovering: It is probable that after the extrusion of eggs, the gonad reverts almost immediately to the immature condition. This stage is, therefore, distinguishable from that found in the immature virgin females only from the size of the prawn.

Observations on the biochemical changes taking place during the gonadial maturation are limited. Read and Caulton (1980) recorded decrease in fresh mass of the animal despite increase in the ovarian mass, and this loss in fresh mass was a function of water loss, as the lipid and protein were seen to increase. Pillay and Nair (1973) observed an inverse relationship between the gonad index and water content during maturation in Metapenaeus affinis. They (Pillay and Nair, 1973) also observed that the lipid and the protein content were maximum during the peak period of gonad development and minimum during the non-reproductive cycle. However, there was no significant fluctuation in the glycogen content. Recently Nagabhushanam and Kulkarni (1982) have shown that in P. hardwickii the mid gut gland reserves were shifted to ovaries during maturation, when glycogen and lipid quantities were increased, but the protein content decreased indicating the conversion of protein to other organic substances to meet the energy requirement during ovarian maturation. In the testes neither the water content nor the lipid showed any relationship with increase in gonad index.

MATING

In the penaeid prawns possessing closed thelyca, mating takes place between hard-shelled males and freshly moulted females. This is to facilitate the insertion of spermatophores in the seminal receptacle in the thelycum. As spermatophores are often encountered in immature females, it is observed that mating in these prawns takes place without any relation to the ovarian development. In the prawns with open thelyca mating normally occurs between hard-shelled males and females.

Courtship and mating behaviour of *P. japonicus* and *P. monodon* have been well described. In *P. monodon* the mating process is initiated when freshly moulted female attracts the hard-shelled males. After a brief period of swimming, one of the males positions himself directly below the female and the pair engages in a parallel swimming movement. Soon the male turns in an upside down position and quickly rotates from this position to a perpendicular position to the female and curves his body to a U-shape around her, and flicks the head and the tail simultaneously. It is believed that during this rotation or shortly afterwards the spermatophore from the male is inserted to the thelycum of the female. In *P. japonicus*, the mating, as recorded by Hudinaga (1942), initiates in the similar manner as observed for *P. monodon*. After moulting, the soft female lays her body sideways and bends ventrad when the male advances to the side of the female and embraces her on her ventral side. The pair then swims with their bodies in an inclined position and during this time the spermatophore is transferred to the thelycum with the help of the petasma.

A lunar rhythm in mating and spawning between the full moon and last quarter of the lunar month was recorded in *M. macleayi* in Australian waters. AQUACOP (1977) observed that in the tropical penaeids, mating occurs earlier on cloudy days and later on sunny days. However, Brown *et al* (1980) recorded the mating in *P. stylirostris* between 14.00 - 15.00 hours regardless of climatic conditions.

SPAWNING

All the cultivable penaeid prawns of this region attain sexual maturity within an year of their life. The size at first sexual maturity recorded in males and females of penaeid prawns of this region is given in Table 1.

Table - 1. Size at first sexual maturity in males and females of cultivable prawns of India

Species	Size(mm) at first maturity male	female
P. indicus	102 TL	130.2 TL
P. semisulcatus	-	23 CL
P. merguiensis	18.5 CL	31.0 CL
P. monodon	37 CL	49 CL
M. dobsoni	53.6 TL	64.1 TL
M. affinis	71.6 TL	80.6 TL
M. brevicornis	-	100 TL
M. monoceros	74 TL	118 TL

TL - Total length; CL - Carapace length.

In nature, all the penaeid prawns, except *M. bennettae*, breed in the sea, although mature males and occasionally maturing females are also encountered in the estuaries and backwaters. Natural maturation and spawning of several species such as *P. merguiensis*, *P. monodon* and *P. indicus* were reported in the enclosed ponds, tanks and raceways provided with sea water. In the wild population, all the penaeid prawns of this region show protracted breeding season with one or two peak spawning periods which are found to vary from place to place and year to year. One of the peak breeding periods coincides with the onset of southwest monsoon and the other with that of the northeast monsoon.

Generally, the smaller species such as *M. dobsoni* and *P. stylifera* breed within 25 m depth region in the inshore sea, while the spawning ground of the larger species (*P. indicus*, *M. monoceros*) is found to extend to 50-60 m depth zone.

The penaeid prawns are capable of spawning more than /in once, and /those on the southwest coast of India, the spawning is found to take place five times in their lives. After each spawning, the individual prawn would again attain sexual maturity within 2 months. The time taken to attain maturity through natural maturation process in captivity is found between 3-4 weeks and 4 months.

The time taken for releasing the eggs during spawning [redacted] relatively short. The eggs are released while swimming in the water near the bottom. During the process of releasing [redacted] eggs, the prawn bends its body posterior to the fourth abdominal segment and shows side-wise movement. The fifth pair of legs are held tight against the body. As there is no muscle tissue in the ovary, it is believed that the r[redacted]se of eggs is brought about by the coordinated contraction of the cephalothoric and abdominal muscles

Read and Caulton (1980) estimated the energy required for egg releasing. They found that the mass and energy difference between the ripe stage IV and the spent stage V was 0.914gand 23.9 KJ respectively indicating the energy content for liberated eggs as 21.85 kJ g^{-1}.

Fertilisation of eggs occurs at the time of spawning. Although the synchronisation of the release of the sperms from the spermatophores as the eggs are released from the ovary is not clearly understood, Oka (1967) believes that in P. orientalis the pressure exerted by the female discharges the sperm which are 'caught' by the eggs as they are liberated. To facilitate the contact of the sperm the eggs extrude jelly-like substance. King (1948), however, opined that the fluid accompanying the egg produces certain chemical or physical effect causing the spermatophore to release the sperm. In P. setiferus it was reported that the gravid females without external spermatophores produced viable eggs in the laboratory. (unpublished report as mentioned in the species synopsis on Penaeus setiferus by M.J. Lindner and H.L. Cook, FAO Fish. Rep., 57 (4) : 144 p (1970).

FECUNDITY

Fecundity or the number of eggs produced by the female prawn is very high and varies from species to species and with the size of the prawn. In the wild, the fecundity of P. indicus and P. semisulcatus ranges from 67,000 to about 700,000 eggs, while in P. monodon from 200,000 to 1 million with an average of 500,000 eggs. P. merguiensis releases approximately 100,000 ripe ova at one spawning. In the species of Metapenaeus occuring in our waters the number of eggs produced varies from 34,000 to 365,000 depending on the species and their size.

FACTORS THAT INFLUENCE MATURATION AND SPAWNING

The most important biological and physiological activity which influence and interact with the maturation of gonads and spawning in the life cycle of the penaeid prawn is moulting. Although these two major metabolic activities compete for the nutrient reserves they are delicately interlinked so that the prawns continue to moult and reproduce. Nevertheless, it is expected that the egg production would reduce the rate at which a prawn could achieve the metabolic status necessary for a moult, thereby extending the intermoult period (Wickins, 1976). Penn (1980) observed that the stages III and IV of ovarian development and the act of spawning were confined to a single intermoult period in *P. latisulcatus*.

Penaeid prawns such as *M. affinis*, *P. stylifera* and *P. maxillipedo* prefer areas of soft mud, rich plankton and and shallow coastal waters for mating and spawning. Among the environmental factors that affect maturation and spawning, salinity is the most important one as it is well known that the penaeid prawns (except *M. bennettae*) migrate from the less saline estuaries and backwaters to the more saline regions of the sea for spawning. Even the reported occurrence of fully mature specimens of *M. dobsoni* and *M. moyebi* and the late mature specimens of *P. indicus* in the backwaters was seen only during the high saline (> 28‰) period. However, the less saline environment of the estuaries and backwaters appears to have no influence on the maturation of testis as mature males are normally encountered in this ecosystem. Salinity around 27 - 36‰ is found to be suitable for maturation of the ovary and spawning.

Although the temperature may not be a limiting factor [illegible] maturation and spawning of penaeid prawns in the tropical waters as prevalent in our country, peak spawning for most of the penaeid prawns off Cochin was observed when the bottom temperature of the inshore ground increased from the lowest in July/August. A temperature range of 22°C - 31°C is found to be suitable for the maturation of gonads and spawning.

Besides salinity and temperature, other factors such as pH and light also influence the maturation and spawning. In the breeding experiments carried out in Polynesia better results were obtained when oceanic water at a pH of 8.2 was used (AQUACOP, 1975). In another series of experiments conducted by Laubier and Laubier (1979) and Caubere *et al*. (1979) it was seen that a light period of 14-16 hours promoted maturation of the ovary.

HORMONAL REGULATION OF REPRODUCTION

Hormonal regulation of reproduction and moulting in malacostracan crustaceans has been reviewed by Adiyodi and Adiyodi (1970). Recently Subramoniam (1981) excellently summarised the present knowledge on the role of hormones in the process of sexualization, gamete formation and emission and in the reproductive strategy of Crustacea. A perusal of these literatures reveal that most of the works carried out on the sexual and reproductive endocrinology of Crustacea relate to non-penaeid prawns, crabs and stomatopods, the studies on penaeid prawns being limited to Laubier (1975), Arnstein and Beard (1975), Kulkarni *et al*. (1979) and Nagabhushanam and Kulkarni (1982).

In crustaceans, the reproductive hormones originate in the neurosecretary organs such as the X-organ/sinus gland complex, protocerebrum and thoracic ganglion and from the non-neurosecretory ovary and androgenic gland (AG). It is now well established that AG hormone is the sex hormone responsible for sex determination of the genetically determined sex in Malacostracan Crustacea. In the presence of this hormone male morphogenesis and spermatogenic activities occur and in its absence female morphogenesis ensues. The activity of AG is controlled by the eye-stalk hormones as well as the protocerebral factors. In gonochoristic forms a single brain hormone maintains the gonadial activity whereas in protandric hermaphorodites two brain hormones regulate the activities.

The moulting and reproductive process in decapod crustaceans are controlled by inhibitor hormones originating from the eyestalk and stimulating hormones, moulting hormone and gonad stimulating hormone from the Y-organ and thoracic ganglion or brain respectively. These hormones act either synergistically or antogonistically along with the moulting and moult inhibiting hormones so that most of the reproductive activity occurs only in the intermoult period. The ovary inhibiting hormone is found in the X-organ/sinus gland complex. Besides these hormones, the ecdysteriods (the ecdysial hormones of crustacea), vitellogenin stimulating ovarian hormone are observed to play important role in ovarian development and vitellogenin. Steroid hormone like 17 hydroxy-progesterone is found to induce spawning in the penaeid prawn *P. stylifera* at a lower temperature of 20°C (Nagabhushanam *et al*., 1982). ~~of 20°C.~~

Recent studies have also shown that the reproductive hormones control the activities of the male and female accessory sex glands and the secretary activities of spermatheca in the oviduct.

CONCLUSION

The foregoing brief review reveals that, although the biological process of reproduction of penaeid prawns are fairly well known, information on the physiological processes and biochemical changes during maturation and spawning is inadequate. Similarly, the role of different environmental factors other than salinity and temperature on the reproductive activities is little understood at present. As the present knowledge on the reproductive endocrine mechanism in the marine penaeid prawns is fragmentary, directed research to elucidate the role of hormones and their complex interaction and influence on the reproduction and somatic growth is imperative to advance intensive culture of these valuable species under controlled conditions.

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